Jackfruit (*Artocarpus heterophyllus* Lam.) Diversity in Bangladesh: Land Use and Artificial Selection[1]

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Jackfruit (*Artocarpus heterophyllus* Lam.) Diversity in Bangladesh: Land Use and Artificial Selection. Bangladesh is often recognized as a secondary center of diversity for jackfruit (*Artocarpus heterophyllus* Lam.) and is expected to harbor important genetic diversity of this underutilized tree crop. Unfortunately, genetic erosion is occurring before this rich local resource has been documented and utilized for potential crop improvement. The aim of this study was to carry out a village-based survey and make morphological measurements to document and assess jackfruit diversity across trees associated with a gradient of three locations/habitats (homesteads, public lands, and forest or fallow lands). We also tested the hypotheses that cultivated jackfruit found in homesteads exhibited positive selection pressure for characteristics desirable in the market, and that the tree location reflected its history of origin and human selection. This was accomplished using 28 standardized morphological descriptors and represents the first large-scale assessment (900 trees) of jackfruit diversity in multiple locations (nine villages). Among the descriptors studied, those most closely associated with jackfruit marketability showed a trend for selection among the trees located in homesteads. Both fruits and leaves were larger in plants on homesteads compared to plants in forest/fallow lands, and fruit quality was significantly higher in homestead trees compared to the other two location categories. However, 18.7% and 23.7% of the fruits found on public lands and forest/fallow lands, respectively, were still considered to be of excellent fruit quality and tree vigor was significantly higher in jackfruit in forest/fallow lands compared to the other location categories. The combination of high tree vigor and presence of excellent fruit quality among jackfruit in forest/fallow lands suggests that the "wild" Bangladeshi jackfruit germplasm, which is considered inferior for market and is being negatively impacted, has valuable genetic diversity to contribute to jackfruit cultivation. Furthermore, sampling across a gradient of habitats may enable the detection of possible trends resulting from domestication pressures.

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বাংলাদেশকে কাঁঠালের (*Artocarpus heterophyllus* Lam.) এর মাধ্যমিক বৈচিত্র কেন্দ্র হিসাবে দেখা হয় এবং এখানে এই স্বল্প ব্যবহৃত বৃক্ষ ফসলের গুরুত্বপূর্ণ জেনেটিক বৈচিত্র বিদ্যমান। দুঃখের বিষয় এই গুরুত্বপূর্ণ জেনেটিক বৈচিত্র তথ্য লিপিবদ্ধকরণ এবং উন্নত জাতের উদ্ভাবনের আগেই ক্ষয়প্রাপ্ত হচ্ছে এবং হারিয়ে যাচ্ছে। এই গবেষণার উদ্দেশ্য একটি গামভিত্তিক সার্ভে ও তথ্য সংগ্রহের মাধ্যমে কাঁঠালের দৈহিক গঠনে বৈচিত্রের একটি তথ্য বিবরণী তৈরী করা যেখানে বৃক্ষসমূহের বিস্তার স্থানীয় অধিবাসীদের মতামতের ভিত্তিতে পছন্দ করে 'রোপিত', 'আধাবন্য' এবং 'বন্য' শ্রেণীভুক্ত করা হয়েছে, যাদের আবাসস্থলের মধ্যেও একটি ক্রমবিস্তার বিদ্যমান যেমন বসতবাড়ীতে, সরকারী জমিতে এবং বন বা পতিত জমিতে। এই গবেষণার উদ্দেশ্য পূরনের জন্য ২৮ টি মান নির্ধারনকৃত বৃক্ষ শারীরিক বৈশিষ্টের বর্ণনাক্রম, এই প্রথম একটি বৃহৎ পর্যায়ের মান নির্ধারণ প্রচেষ্টায় (৯০০ বৃক্ষ), বহু সংখ্যক (নয়টি গ্রামের) আবাস স্থলে পরিচালনা করা হয়। যে সমস্ত অর্ন্তভূক্ত বর্ণনা-বৈশিষ্ট কাঁঠালের বাজার মূল্য নির্ধারনের সঙ্গে সংশিষ্ট, সেগুলির মধ্যে নিবাচনের একটি ধারা পরিলক্ষিত হয়েছে এবং এদেরকেই 'পছন্দ করে রোপিত' শ্রেণীভুক্ত করা হয়েছিল। বসতবাড়ীতে রোপিত বৃক্ষসমূহের পাতা ও ফল উভয়েই বনাঞ্চল ও পতিত জমিতে পাওয়া বৃক্ষের চেয়ে বড় হতে দেখা গেছে, ফলের গুনগত মান ও অন্যান্য দুই শ্রেণীর থেকে 'রোপিত' শ্রেণীতে উৎকৃষ্ট, অবশ্য যথাক্রমে ১৮.৭% এবং ২৩.৭% 'আধাবন্য' এবং 'বন্য' ফল অত্যন্ত সুস্বাদু গুনের বলে পছন্দ করার মত আর 'বন্য' কাঁঠালের বৃক্ষের আকার ও সতেজতা 'রোপিত' বৃক্ষের থেকে তাৎপর্যপূর্ণভাবে উন্নত। 'বন্য' ও 'আধাবন্য' জাতের কাঁঠাল বৃক্ষের উৎকৃষ্ট আকার ও সতেজতা এবং কিছু ফলের উৎকৃষ্ট গুণ সম্পন্নতা এটাই প্রমান করে যে, বাংলাদেশের এইসব বনাঞ্চল ও পতিত জমির 'বন্য' ও 'আধাবন্য' জার্মপাজম যেগুলি ঢালাওভাবে বাজারে কম গুন সম্পন্ন বলে চিহ্নিত, তা থেকে মূল্যবান উৎকৃষ্ট কাঁঠালের জাত বাছাই ও চাষের জন্য গুরুত্বপূর্ণ ভূমিকা রাখতে পারে। তাই এই জার্মপাজম এর তথ্য লিপিবদ্ধকরণ এবং সংরক্ষণ অত্যন্ত জরুরী। কৃষকদের নিজ বসতবাড়ী ও জমিতে এবং জার্মপাজম সংগ্রহশালায় অনতিবিলম্বে এটা করা প্রয়োজন।

Key Words: Jackfruit, *Artocarpus heterophyllus*, Bangladesh, genetic erosion, on-farm conservation, underutilized crops.

Introduction

Plant Genetic Resources (PGR) represent the raw materials that farmers and plant breeders use to improve the quality and productivity of their crops. There is worldwide concern over the ever-increasing loss of PGR diversity, especially of underutilized crops (Williams and Haq 2002). A major reason for this is the replacement of diverse, genetically variable landraces with a few genetically uniform modern varieties (Brush 1991; Harlan 1992; Hawkes 1983; NRC 1993). On-farm or *in situ* conservation has been advocated as an important way to conserve diversity

(Oldfield and Alcorn 1987; Brush 1991; IPGRI 2000). On-farm conservation of PGR is the continued cultivation and management of a diverse set of crop populations by farmers in the agro-ecosystems where the crop has evolved. It is dynamic and is aimed at maintaining the evolutionary processes that continue to shape diversity. Conservation, sustainable use, and the open exchange of underutilized crops will be crucial in feeding the world's growing population. Bangladesh and surrounding regions are among the most populous in the world and are rich in important PGR. Cultigens and wild genotypes of underutilized crops in this region must be identified and assessed for genetic diversity and ensured for *in situ* conservation for long-term sustainable use and conservation (Haque 1991).

Jackfruit (*Artocarpus heterophyllus* Lam.), the national fruit of Bangladesh, is a good example of a highly diverse local resource whose genetic base is being threatened. It is a large monoecious tree producing often enormous (up to 50 cm×100 cm and weighing up to 50 kg, Jagadeesh et al. 2006; Jarrett 1959) multiple fruits that are cauliflorous (Fig. 1). The tree produces high quality timber, leaves are used for fodder, and the fruit is consumed by humans. It may be eaten fresh, cooked, or processed into juices, ice creams, or chips. In Bangladesh, uniform and high yielding exotic genotypes are replacing genetically diverse stands, and genetic variation is gradually being lost for the sake of increased production (Haque 1991). In 1992, the Commonwealth Science Council (CSC) and the International Centre for Underutilized Crops (ICUC) held a workshop in Dhaka, Bangladesh that was designed to identify and develop plans for promoting the cultivation, processing, and conservation of underutilized crops that are already cultivated locally. Jackfruit was identified as deserving priority attention in Bangladesh because it is already an important and diverse crop there (Azad et al. 2007; Hossain 1996; Saha et al. 1996), and Bangladesh is considered a secondary center of jackfruit diversity (Arora 1998; Dhar 1998; Hossain 1996). This study focuses on assessing morphological descriptors of jackfruit in Bangladesh across a range of locations to better understand jackfruit diversity as well as inform *in situ* conservation strategies.

Fig. 1. Cauliflorous male and female inflorescences of a jackfruit tree. Scale bar is 5 cm.

Jackfruit Origins

The place of origin and wild ancestor of jackfruit is unknown. Jackfruit has been cultivated for millennia and was referred to as early as 300 B.C.E. by Theophrastus (Hort 1916). It is now so widely cultivated that the region in which it is indigenous and its wild progenitor is unclear. Today it can be found in cultivation at low elevations from the Indian subcontinent through Bangladesh, Myanmar, into southern China, Laos, Vietnam, Cambodia, Thailand, Malaysia, Indonesia, and Oceania. It is also commonly cultivated in the Philippines, and has been introduced throughout Africa and the Neotropics. It has been under cultivation for so long that Jarrett (1959) speculated it would not be possible to identify the wild progenitor. It is, nevertheless, believed to be native to the Indo-Malaysian region (Beddome 1873; Brandis 1906; Gamble 1902; Kanjilal et al. 1940; Talbot 1911; Wight 1843). More specifically, jackfruit is often considered to originate from the Western Ghats of India as Wight (1843) reported finding trees growing in primary forest away from human habitation. Barrau (1976) suggested that it originated in Malaysia due to the great diversity of jackfruit cultivars found there. While jackfruit

is important and widely cultivated in Malaysia, it was likely introduced there and never found in the wild (Jarrett 1959).

Bashar and Hossain (1993) suggest that wild jackfruit relatives inhabit the Andaman Islands and report that it is found only under cultivation in Bangladesh. However, it is often found in forests in Bangladesh away from human habitation (Zuberi, pers. observation). In many districts like Tangail, Mymensingh, Dhaka, and adjoining areas, many jackfruit trees grow in the wild near and in forest edges and fallow lands. Many of these trees grow tall and bear relatively small but numerous fruits that are, in most cases, inedible or of very poor quality. The local people call these "*jangli kathal*" (wild jackfruit).

A wide and undocumented diversity of jackfruit has been observed throughout Bangladesh, but little attention has been paid to the documentation and conservation of its genetic resources. This documentation is crucial to better understand the history of jackfruit domestication. If Bangladesh is a "secondary center of diversity" for jackfruit, this implies that it was domesticated elsewhere and subsequently introduced to Bangladesh, where the crop was then diversified. If there truly are wild jackfruit trees in Bangladesh, then it is possible that Bangladesh is part of a broader center of origin of the crop (a "non-center," sensu Harlan 1971). On the other hand, perhaps the trees growing in forests and fallow lands that exhibit "wild" characteristics are not truly ancestrally wild, but rather represent naturalized feral populations of trees that in the absence of human selection evolved back toward wild characteristics after the crop was introduced to the area millennia ago. Before these questions can be addressed, a better understanding of the morphological diversity of Bangladeshi jackfruit is necessary.

Jackfruit Diversity

Being a multipurpose tree that yields food, fodder, timber, and fuel, jackfruit has played an important role in the rural economy of Bangladesh. Jackfruit trees are common in almost every household in Bangladesh. However, reports indicate that a moderate level of genetic erosion of jackfruit diversity has already occurred in Bangladesh (Khan 2008; Zuberi, pers. observation). In addition to the loss of jackfruit trees due to logging and clearing land for agriculture, market demand for jackfruit may lead to the replacement of local diversity with uniform exotic genotypes and to the replacement of local consumption with sales to large urban markets. As a cross-pollinated and seed-propagated species, jackfruit population diversity results from the breeding system and natural selection associated with local environmental differences (evolution) or from human selection and the preferences of the local community cultivating them (domestication). As an underutilized crop, jackfruit has escaped intensive selection and cultivation. For these reasons, a wide range of genetic and morphological variation has been reported for jackfruit (Azad 1999; Azad et al. 2007; Hossain 1996; IPGRI 2000; Jagadeesh et al. 2006; Saha et al. 1996; Schnell et al. 2001; Shyamalamma et al. 2008; Ullah and Haque 2008). All of these studies indicate that both within and between population variation exists. These studies have, however, been limited in geographical scope and in the number of individuals examined, as very few germplasm collections of jackfruit are known (IPGRI 2000).

Objectives

The genetic diversity of jackfruit is a valuable resource for the present and future. Bangladesh is expected to be home to rich morphological and genetic variability, and possibly harbor wild jackfruit. The documentation of this genetic resource is a necessary first step in understanding and conserving the diversity for long-term sustainable use. The aim of this study was to carry out a village-based survey within a region where a rich variability of jackfruit is expected and to document jackfruit morphological diversity across trees in a gradient of locations (homesteads, public lands, forest/fallow lands). This was accomplished using morphological standardized descriptors (IPGRI 2000), and it represents the first large-scale *in situ* assessment (900 trees) of jackfruit diversity in multiple locations (nine villages). It is hypothesized that jackfruit populations will show genetic diversity reflected in morphological variation as adaptations to different local environmental (i.e., location) and human selection pressure. We hypothesize that jackfruit intentionally planted on homesteads will exhibit positive selection pressure for characteristics desirable in the market, and that the location of a tree will reflect its history of origin and human selection (e.g., trees near forested areas and fallow lands are more likely to be plants with little or no human selection, whereas in villages with new and more

concentrated homesteads "wild" trees have been removed and new more desirable types have been planted). Examination of morphological variation will help determine the phenotypic expression of the genetic variation present. The results will provide baseline data on diversity of jackfruit genetic resources in Bangladesh, shed light on morphological variation due to the pressure of cultivation and selection in the villages, and will be used to develop the framework for a molecular level study of Bangladeshi jackfruit diversity in an effort to combat the erosion of genetic diversity.

Material and Methods

Study Site

The study was conducted in the district of Tangail of Bangladesh (Fig. 2) in nine villages (Table 1) where the authors have good rapport with villagers and where jackfruit trees grow widely in villages and forest edges. The villages form a transition from forested areas with very scattered human settlements to densely populated villages away from forest and fallow lands. Land use types include farming (about 50%), forest (20%), and homesteads (15%). The study area falls broadly within the region of semi-deciduous forest dominated by sal (*Shorea robusta* Roxb. ex Gaertn. f.). This area has a long history of human habitation, so it is not possible to know exactly the past history of land use in areas that are now forest or fallow lands. It is possible that these lands were managed in the past. However, the indigenous people still inhabit the study area and they did little alteration to the forest until the 20th century. The homesteads included in this study represent "settlers" who cleared parts of the forests for croplands and settlements starting in the 20th century. It is likely that the jackfruit and other tree species in and around forests are remnants from before this time.

Village Interviews

In the selected areas, 120 villagers were asked in unstructured interviews about the history and origin of individual jackfruit trees in their homestead, neighborhood, fallow lands, and in the forest (Table 1). Both males and females of varying ages were surveyed. However, given that many people do not know their age and women are reluctant to answer questions about their age, the exact ages of individuals were not gathered. Villagers were asked questions from a checklist in informal group discussions, regarding a particular tree. In the survey questions, stress was placed on the age and qualitative characteristics of the trees following recommendations from the International Plant Genetic Resources Institute's "Descriptors for Jackfruit" (IPGRI 2000). They were also asked about fruit quality, taste, and size as well as about their use of jackfruit. This was accomplished by having the group taste the available fruit of the tree they were examining and rank its quality following IPGRI descriptors (2000). Tree vigor was measured following the recommendations of IPGRI (2000) on a three point scale (low, medium, high). Tree vigor was assessed by the first author after she had done a field survey and standardization trial.

Assessments of jackfruit trees were made based on three broad location categories: Trees found on small homesteads (known to be intentionally planted by humans), trees found on public land (not known whether or not they were intentionally planted), and trees found away (at least 2/3 km) from the homesteads in fallow lands, forests and forest edges (were not planted by the villagers). The three categories will be referred to as "Homestead," "Village," and "Forest/Fallow," respectively. These three location-based categories were used in the present study to assess morphological diversity of jackfruit across a gradient of trees and habitats in a narrow geographic range. Within each category, 300 adult jackfruit trees were chosen randomly from across the nine villages, for a total of 900 trees sampled (Table 1).

Assessment of Variation

Morphological variation among trees was assessed using jackfruit descriptors from the International Plant Genetic Resources Institute (IPGRI 2000). Descriptors included 20 qualitative and eight quantitative measures of vegetative and reproductive characters (Tables 2 and 3). The qualitative tree characters were measured by observation and drawing upon the knowledge of the local villagers. Quantitative characters were measured in centimeters (Table 3). Statistical analyses were performed using JMP 5.1.2 (SAS Institute, Cary, North Carolina, USA). The quantitative data were analyzed using one-way ANOVA and Principal Components Analysis

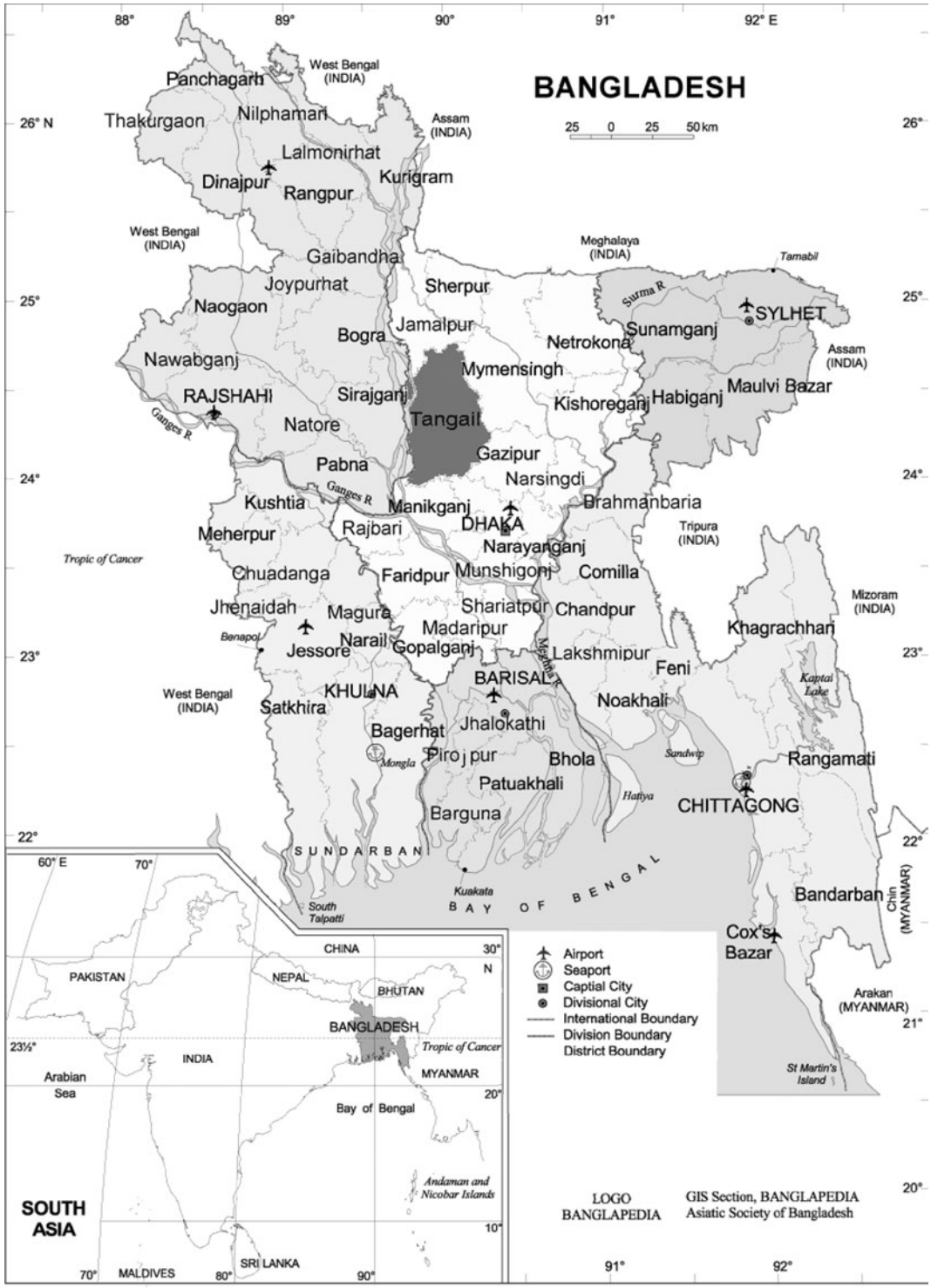

Fig. 2. Map of Bangladesh indicating Tangail district in dark gray.

TABLE 1. VILLAGES AND VILLAGERS SURVEYED FOR JACKFRUIT DIVERSITY.

				Villagers Interviewed		
Unions	Villages	Area (hectares)	Population	Young Males	Old Males	Females
Arankhola	Chunia	1,392	4,041	7	5	9
Aushrara	Idilpur	176	738	3	3	6
	Haldia	2,167	1,472	6	4	5
	Mahishmara	125	5,844	9	6	13
Alokdia	Trngri	153	1,285	3	3	4
	Akadi	406	1,617	2	1	2
	Raniad	113	3,152	1	1	2
	Sathibari	217	921	4	3	5
	Digarbaid	4,972	1,699	5	4	4
Total	9	9,722	20,769	40	30	50

(PCA). For qualitative data, frequency distribution analyses and chi-square tests were performed.

Results

VILLAGE INTERVIEWS

Interviews in nine villages in the Tangail District of Bangladesh indicated that the diversity of tree species in the homesteads of this district had declined drastically during the last five decades. Many homesteads reported that they had sold most of their large trees for timber and that the naturally growing trees in the forest and fallow lands (ones that were not planted by humans) had almost disappeared. The tall, mature jackfruit trees were cut as part of land clearance efforts and marketed as timber. Increased demand and high prices convinced villagers to sell the large mature trees, and they were not replanted. Instead, exotic trees like mahogany, *Eucalyptus*, and *Acacia* were planted due to their promotion by the authorities.

Interviews also demonstrated the importance of jackfruit and the recognition of wild diversity of the jackfruit (*kathal)* tree. Villagers ranked it as the second most important tree crop on their homesteads after mango, and villagers were

TABLE 2. QUALITATIVE CHARACTERS INCLUDED IN STUDY.

Character Name	Character States
Tree vigor	Low, medium, high
Age of tree	Juvenile (5–10 y), young (11–19 y), medium (20–29 y), old (30–39 y), mature (40+ y)
Canopy structure	Pyramidal, broadly pyramidal, spherical, oblong, semicircular, elliptical, irregular
Branching density	Sparse, medium, dense
Branching type	Slender main trunk with few branches on top, main trunk medium with several thick branches, main trunk short with many branches from base
Trunk surface	Smooth, rough, very rough
Branching pattern	Erect, opposite, verticillate, horizontal, irregular
Leaf blade shape	Obovate, elliptic, broadly elliptic, narrowly elliptic, oblong, lyrate
Leaf apex shape	Acute, acuminate, retuse, obtuse
Leaf base shape	Oblique, rounded, cuneate, shortly attenuate
Leaf texture	Thick smooth, thick rough, medium, thin smooth, thin rough
Leaf color	Light green, green, dark green, pinkish green
Fruit bearing position	Main trunk, primary branch, secondary branch
Fruit shape	Obloid, spheroid, ellipsoid, clavate, oblong, irregular
Stalk attachment to fruit	Depressed, flattened, inflated
Fruit rind color	Green, greenish yellow, yellow, reddish yellow
Fruit surface	Smooth, spiny
Shape of fruit spine	Sharp pointed, intermediate, flat
Spine density	Sparse, dense
Fruit attraction	Poor, intermediate, good, excellent

TABLE 3. SUMMARY OF VARIATION OF QUANTITATIVE CHARACTERS AMONG THREE CATEGORIES OF JACKFRUIT TREES BASED ON ANOVA. THE MEANS (STANDARD DEVIATION) ARE INDICATED IN CENTIMETERS FOR EACH CHARACTER.

Character	Homestead	Village	Forest/Fallow	Significance
Tree (dbh)	79.89 (39.36)	114.54 (42.24)	132.64 (42.86)	<0.0001*
Leaf blade length	13.13 (2.73)	13.08 (2.19)	13.16 (2.52)	0.9281 n.s.
Leaf blade breadth	11.32 (2.53)	9.70 (2.29)	8.97 (2.03)	<0.0001*
Leaf tip length	3.23 (2.79)	2.13 (1.64)	1.96 (1.08)	<0.0001*
Fruit stalk length	7.60 (1.65)	6.80 (1.09)	6.67 (0.93)	<0.0001*
Fruit stalk diameter	13.53 (1.77)	12.11 (1.88)	9.12 (2.35)	<0.0001*
Fruit length	56.82 (16.91)	47.38 (18.31)	35.11 (9.85)	<0.0001*
Fruit diameter	165.18 (43.02)	117.23 (45.58)	66.61 (17.40)	<0.0001*

especially cognizant of the wide variation in fruit quality. Several names were used to describe this variation, including "*chaila kathal*" (hard, tasteless jackfruit), "*roachhara kathal*" (jackfruit without "roa" or pulp), "*hazari kathal*" (bearing a thousand small fruits), "*khokra kathal*" (wavy, irregular shaped, tough fruit), and "*neisha kathal*" (very soft, sweet, small-sized pulp). These names indicate plants that are somewhat "wild" or not entirely domesticated. These are considered inferior in quality and generally are not preferred or have a low price in the market. However, such trees are still kept for timber and wood, and poor people use these inferior fruits as "green vegetables" before they reach maturity.

The villagers typically plant jackfruit trees that produce high quality fruits for human consumption in their homesteads. They keep the naturally generated jackfruit trees of poor fruit quality in the pineapple orchards and edges of farmlands for timber because they grow rapidly and achieve tall stature. The villagers also noted that jackfruit trees in "*Chala*" (Uplands) of the region near forests occurred naturally when they came to settle there, but they have since been removed for timber.

ASSESSMENT OF VARIATION

All of the qualitative characters measured exhibited wide variation. For each category (homestead, village, and forest/fallow), every possible character state was present for each of the 20 qualitative characters. For most of the characters, the patterns were similar across plant categories (data not shown) and there were no apparent trends. However, fruit attraction and tree vigor were among the few characters with significant differences between categories. For forest/fallow and village trees, "good" quality fruits were the most numerous, while among homestead trees "excellent" quality fruits were the most numerous (Fig. 3a). The number of "excellent" fruits was significantly higher ($p=0.0043$) in homestead trees compared to both village and forest/fallow trees, between which there was no significant difference (Fig. 3b). For tree vigor, forest/fallow trees were significantly ($p=0.0194$) more vigorous than either village or homestead trees (Fig. 4).

Among the four quantitative tree and leaf characters, all except one (leaf blade length) showed significant differences among tree categories (Table 3). For the diameter at breast height (dbh), there was a significant difference in size; forest/fallow trees were the largest and homestead trees were the smallest. Although heavily fruiting homestead trees may have somewhat less vegetative growth than trees with less fruit load, this still suggests that the forest/fallow trees are older and the homestead trees are more recently planted. This agrees with the age assessments of the trees based on interviews with villagers. The other two leaf characters showing significant differences are leaf blade breadth and leaf tip length with a progression from largest to smallest from homestead to village to forest/fallow.

Among the four quantitative fruit characters, all showed significant differences among tree categories. In all cases the homestead trees had larger fruits and fruit stalks, followed by village, and the forest/fallow trees had the smallest dimensions (Table 3).

A principal components analysis was performed on the quantitative data in order to visualize how the individual trees in the three categories are associated with one another and to determine what characters best explain this association. Since dbh is indicative of the age of a tree, this character was excluded. Based on the

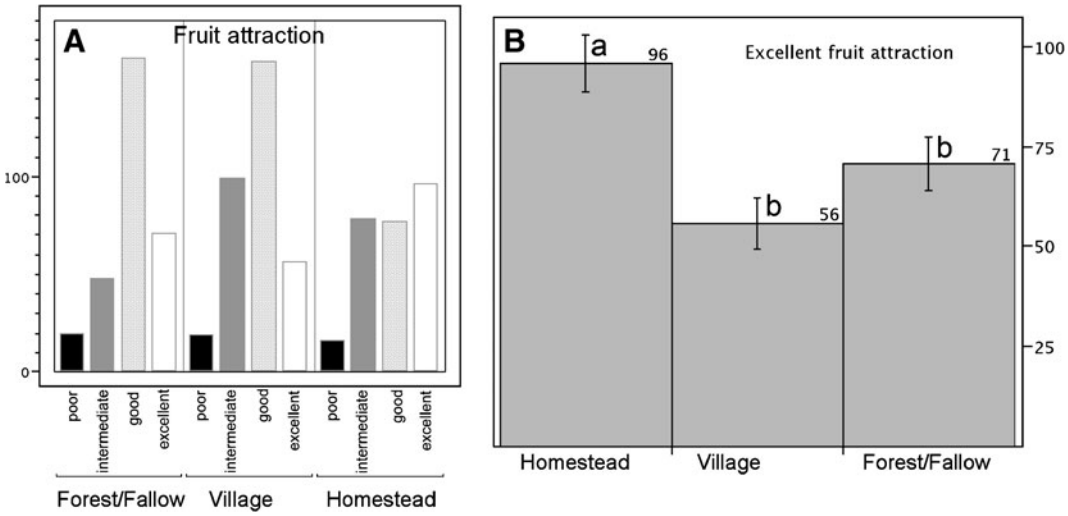

Fig. 3. Levels of jackfruit fruit attraction. A) Distribution of fruit attraction levels among 300 each (total 900) of forest/fallow, village, and homestead jackfruit trees. The y-axis indicates the number of trees. B) Histogram of the number of trees with excellent fruit attraction from among 300 each (total 900) of homestead, village, and forest/fallow jackfruit. Bars indicate standard error. Different letters above bars indicate a significant difference ($p<0.05$).

remaining seven characters, trees from each category overlap, but there is a clear progression from forest/fallow to village to homestead trees, with fruit length and fruit diameter explaining 93.6% and 5.8% of this association, respectively (Fig. 5). As there are positive correlations between fruit length and fruit diameter ($r^2=0.364$) as well as between fruit length and fruit stalk length ($r^2=0.280$), the data are not completely independent. However, when fruit length is removed from the PCA, the results are the same, that is, there remains a clear progression from forest/fallow to village to homestead trees. But rather than fruit length explaining the majority of this association, fruit stalk diameter and leaf breadth explain 31.2% and 20.7%, respectively.

Discussion and Conclusion

Because jackfruit is almost entirely cross-pollinated, this long-lived, woody tree species is expected to exhibit large within-population variation (Hamrick and Godt 1990). Not surprisingly,

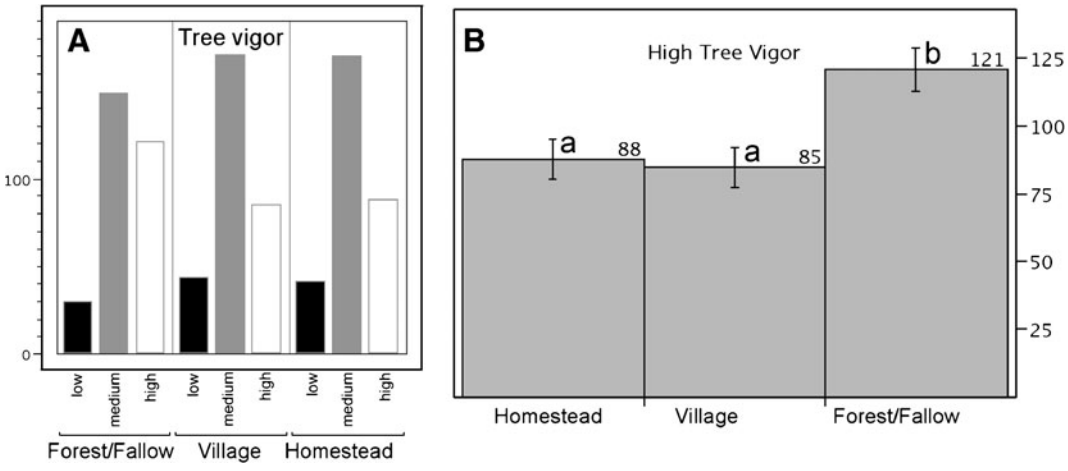

Fig. 4. Tree vigor in jackfruit. A) Distribution of tree vigor levels among 300 each (total 900) of forest/fallow, village, and homestead jackfruit trees. The y-axis indicates the number of trees. B) Histogram of the number of trees with high tree vigor from among 300 each (total 900) of homestead, village, and forest/fallow jackfruit. Bars indicate standard error. Different letters above bars indicate a significant difference ($p<0.05$).

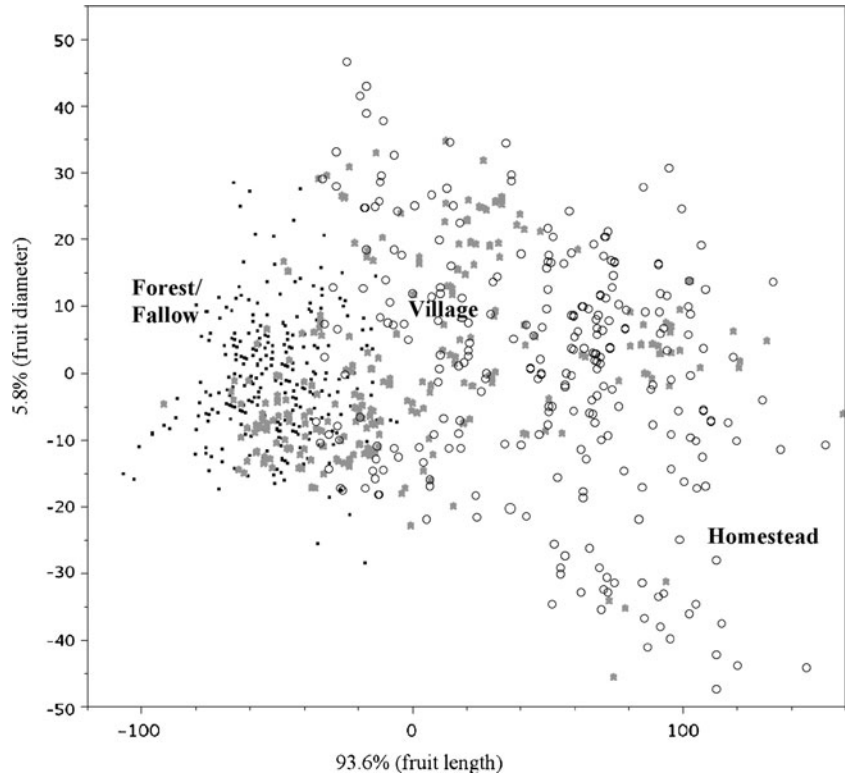

Fig. 5. Principle component analysis of seven quantitative characters. Symbols are as follows: homestead (open circles), village (gray stars), and forest/fallow (black dots).

great variability was observed both within and between categories for most of the characters. However, the data presented here demonstrate significant differences across the three categories of trees, in six of seven quantitative measurements (excluding dbh, which is indicative of tree age) (Table 3). This supports the categorization of jackfruit trees in this region into three morphologically distinct classes associated with their location (homesteads, village – close to habitations but on public land, and forest/fallow). It also suggests that there is unique genetic diversity harbored in each of these populations. This diversity should be targeted for conservation and may be indicative of the history of origin of the trees. The differences between the populations could possibly be due to the "wild" and "semi-wild" trees (of the forest/fallows and villages, respectively) having escaped from the constraints of human selection such that they revert to "wild" phenotypes. However, since the area of origin for domesticated jackfruit remains unknown, the presence of this "wild" germplasm is significant and could truly represent semi-wild (village) and wild (forest/fallow) jackfruit germplasm, respectively.

Considering both quantitative and qualitative data, a trend for selection in homestead jackfruit populations was observed. The plants from the three categories showed a pattern of variation that may be explained by domestication pressures. Specifically, both leaves and fruits were larger in cultivated plants on homesteads compared to "wild" plants in forests and fallow lands (Table 3), and fruit quality was significantly higher in homestead trees compared to the other two categories (Fig. 3). As the leaves of some tree species may have larger leaves in younger individuals, correlation between age (as indicated by dbh) and the leaf size characters were tested. There were no significant differences between these characters, suggesting that the trend toward larger leaves in the homesteads is not age related. As the villagers are growing trees for market on their homesteads, fruit quality and size are important and there appears to be a strong selection for larger, higher quality fruits among the homestead trees.

Nonetheless, 18.7% and 23.7% of the village and forest/fallow fruits, respectively, were still considered to be of excellent fruit quality (Fig. 3b), indicating that these categories of trees still have potential for the market. Interestingly, tree vigor, which is important for the long-term survival of a tree, does not seem to be under selection by humans among the homestead trees. Forest/fallow trees are significantly more vigorous than either homestead or village trees (Fig. 4). With the combination of high tree vigor and presence of some excellent quality fruit among forest/fallow jackfruit, this suggests that the "wild" germplasm, which is considered inferior for market, has valuable genetic diversity to contribute to jackfruit cultivation and should be conserved.

While there are a few key characters, described above, that seem to be under positive human selection, most of the characters show no clear pattern or trend across forest/fallow, village, and homestead trees. This indicates that jackfruit is a highly variable tree crop and its domestication has not progressed much in Bangladesh. However, the results suggest that the process of domestication is ongoing and supports the hypothesis that the location of trees can reflect their history of human selection with trees away from human habitation (i.e., in forested areas and fallow lands) being under little or no human selection, but harboring valuable "wild" genetic diversity, such as high tree vigor. These valuable genetic resources may be incorporated in cultivation through plant breeding efforts. Unfortunately, in villages with new and more concentrated homesteads, "wild" trees are often replaced by a few, more genetically uniform varieties desirable for market. Given that Bangladesh has identified jackfruit as a priority underutilized tree crop for improvement, identifying and utilizing the full range of its genetic diversity will be important. Sampling along transects with a direction of transition from concentrated human settlements to areas away from human habitation may result in the identification of valuable "wild" jackfruit genetic diversity. In the current study, the sampling from three different types of habitats enabled the detection of possible trends resulting from domestication.

Indigenous knowledge was of crucial importance in this study. Interviews indicated that villagers clearly use characters of fruit size and quality to identify jackfruit trees that have not been intentionally planted. The villagers definitely prefer the fruits of the homestead trees to those of the naturally regenerating "wild" trees. They remove the wild trees from their homesteads and replace them with trees producing higher quality, larger fruits. The findings highlight areas of concern and promise for jackfruit in Bangladesh. The small, inferior fruit types face high rates of genetic erosion as people opt for taste and size. Old, naturally generated trees with large tree structure and high tree vigor are rapidly being lost because of their market value for timber, yet they harbor valuable genetic diversity. In rural villages throughout Bangladesh, small farmers depend largely on the local natural resources, comprising an integrated agroecosystem of diverse field vegetables, fruit crops, and trees. Sustainable agriculture and development under complex, diverse, poverty stricken, risk prone, village-based conditions, like monsoon Asia, requires a more resilient traditional system that depends upon diversity, both in terms of genetic variability as well as diversity over time and space in the farming system. Thus, the use of local crops and trees, like jackfruit, with high genetic variability in the traditional systems should be preserved and revitalized.

The current results and villagers' knowledge base indicate that Bangladesh could harbor wild jackfruit diversity and represent a noncenter or secondary center of diversity. This highlights the need in Bangladesh for A) further documentation and evaluation of jackfruit fruit types, B) development of a subset of representative descriptors for different jackfruit plant and fruit types that will facilitate ease of use by local researchers and farmers, C) identification of preferred jackfruit cultivars, D) molecular assessment of jackfruit diversity in a larger context compared to other regions, and E) establishment of jackfruit germplasm collections as well as participatory on-farm conservation programs. Most of the villagers expressed their willingness to participate in any plant conservation program, but they emphasized that it would have to be part of a well-defined, long-term program with the involvement of the government or non-governmental organizations to insure long-term sustainability.

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